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Germination and Emergence of Primed Grass Seeds Under Field and Simulated-field Temperature Regimes

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Seed priming may enhance establishment success of cool-season range grasses which must compete with annual weeds for early spring moisture. Previous priming studies have confirmed germination rate enhancement for these species but relative treatment effects under field-temperature conditions have not been assessed. We primed seeds of thickspike wheatgrass [*Elymus lanceolatus* (Scribn. and J. G. Smith) Gould], bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) Löve], Sandberg bluegrass (*Poa sandbergii* Vasey.) and bottlebrush squirreltail [*Elymus elymoides* (Raf.) Swezey] and evaluated their relative emergence rate in three soil types as a function of spring-planting date. Germination response was simultaneously evaluated in laboratory germinators that were programmed to simulate the field-temperature regime at planting depth. Seed priming enhanced both germination and emergence rate with the greatest effect occurring during the earlier, cooler planting dates. Total emergence and emergence rate in the field were lower than for the equivalent germination response in the laboratory. Thermal-germination response was modelled and predictions developed for evaluating potential germination under late winter/early spring soil-temperature regimes. Modelling results predicted that greater germination enhancement would have been possible at earlier planting dates than were measured in the field experiment.

Key words: Bunchgrass, germination, emergence, priming, rate, temperature.

INTRODUCTION

Seed priming is a pre-germinative treatment in which seeds are held at a water potential that allows imbibition, but prevents radicle extension (Bradford, 1986). Priming has been shown to increase low-temperature germination rate and subsequent field emergence for many crop species (Taylor *et al*., 1998). Keller and Bleak (1968) and Bleak and Keller (1970, 1972, 1974) used a wetting-and-drying seed treatment to enhance field establishment of several rangeland grasses, but most priming studies of similar species have been limited to laboratory tests (Hardegree and Emmerich, 1992; Hardegree, 1994*a*,*b*, 1996; Mueller, 1996). Hardegree (1994*a*,*b*, 1996) suggested that an increase in low-temperature germination rate might prove beneficial to establishment of cool-season range grasses, which must compete with annual weeds for early spring moisture.

Thermal-germination models can be used to quantify the temperature dependence of seed germination and emergence (Probert, 1992). Hardegree and Van Vactor (1999) used a model to describe germination response of several rangeland grass species under simulated-field-temperature regimes but did not evaluate model response in the field. Field emergence is affected by a number of biological, physical and chemical factors in addition to those that can be attributed to temperature (Hegarty, 1973; Egli and TeKrony, 1996; Weaich *et al*., 1996).

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Hardegree and Burgess (1995) developed a germination-control system that allows for laboratory simulation of field-temperature regimes in near-real time. Simultaneous measurement of field emergence and laboratory germination may reveal new insights regarding the relative influence of temperature and other environmental factors on seedling establishment. The purpose of this study was to measure priming effects on germination and emergence of several perennial bunchgrasses native to the Great Basin region of the western United States. Specific objectives were: (1) to evaluate priming effects on both germination and emergence under field, and simulated-field temperature regimes; (2) to develop models to characterize cumulative germination response to temperature; (3) to compare laboratory germination and field emergence patterns under identical temperature regimes; and (4) to estimate seed-priming effects on germination response under alternative field-temperature scenarios.

MATERIALS AND METHODS

Thickspike wheatgrass [*Elymus lanceolatus* (Scribn. and J. G. Smith) Gould], bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) Löve], Sandberg bluegrass (*Poa sandbergii* Vasey.) and bottlebrush squirreltail [*Elymus elymoides* (Raf.) Swezey] seeds were purchased from a commercial source which collected the seeds in 1991 and 1992 for experiments conducted in 1993 and 1994, respectively. Seeds were stored in cloth bags at room temperature between collection and use. These species were selected because they

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have been identified by the United States Department of the Interior, Bureau of Land Management as high-priority species for restoration of deteriorated rangelands in the Intermountain region of the western United States.

Seeds were primed using the matric-potential control system described by Hardegree and Emmerich (1992). A preliminary experiment was conducted to estimate the optimal-priming conditions of water potential and treatment duration for these seedlots following the procedure suggested by Hardegree (1996). Optimal priming conditions for 1991 seeds were determined to be 4 d equilibration at −1·0 MPa for thickspike wheatgrass, −1·6 MPa for bluebunch wheatgrass, −1·3 MPa for bottlebrush squirreltail, and −1·0 MPa for Sandberg bluegrass. Optimal priming conditions for 1992 seeds were determined to occur after a 6 d equilibration at −1·3 MPa for thickspike wheatgrass, −1·6 MPa for bluebunch wheatgrass, −1·3 MPa for Sandberg bluegrass, and after a 4 d equilibration at −1·3 MPa for bottlebrush squirreltail. Seeds were primed at 25°C, air-dried on the laboratory bench for 1 week and then stored in cloth bags at room temperature until needed (Hardegree, 1994*b*). Seeds were primed 2 weeks in advance of the first germination test in a given year.

Field emergence

Primed and non-primed seeds were planted, and seedling emergence monitored, in field plots located on sandy loam (55% sand, 38% silt, 7% clay; site 1), loamy sand (79% sand, 17% silt, 4% clay; site 2) and silt loam (27% sand, 58% silt, 15% clay; site 3) soil types at the Orchard Field Test Site in southeastern Ada County, Idaho. Emergence plots on each soil type were instrumented with at least three thermocouples for recording soil temperature at a depth of 1 cm. Soil temperatures were monitored every 10 min and average temperatures calculated for each hour of the field experiment. Data were recorded by an automated data acquisition and telemetry system that transmitted the data to the Boise laboratory every morning.

One hundred and fifty seeds of each species and treatment were planted in each of three 10 × 20 cm bare-soil micro-plots in each soil type on 1 April and every 10 d thereafter, for a total of six planting dates in each year. Micro-plots were arranged in three randomized blocks on each soil type. Blocks were hand irrigated every second day to reduce water stress as an environmental variable. Each block was visited every 2 d for 28 d after planting and checked for emergence. Newly-emerged seedlings were counted and removed.

Laboratory germination

Seeds were germinated in the same matric-potential control system used for priming (Hardegree and Emmerich, 1992). Matric-potential control was not a factor in the germination study so the solution reservoir inside the germination vials contained water rather than an osmotic solution. Free water on top of the membrane was minimized by maintaining the solution reservoir at the same height as the membrane and by daily suction when necessary. Seeds were dusted with Daconil fungicide powder (2,4,5,6-tetrachloro-1,3-benzenedicarbonitrile, wettable powder) at the beginning of a given experimental run and as needed thereafter to control fungal-deterioration of the membrane.

Temperature control was maintained inside 15 programmable-environmental chambers of the type described by Hardegree and Burgess (1995). A computer monitoring and control system evaluated chamber temperature every 3 min and adjusted the temperature whenever measured temperature deviated from programmed temperature by $\geqslant 0{\cdot}5$°C. A datalogger monitored chamber temperature every 10 sec and recorded an average temperature value for every 15 min period. Chamber lights, which maintained a photon irradiance of $16{\cdot}0 \pm 0{\cdot}4$ μmol m^{-2}, were activated for 12 hd^{-1} starting at 0600 h.

Laboratory germinators were programmed to simulate thermal conditions in the field-emergence plots at the Orchard site. Laboratory-germination experiments were conducted simultaneously with field-emergence experiments but with a 3 d lag-time in 1993, and a 5 d lag-time in 1994. The thermal lag was maintained so that germination and emergence measurements could be made on alternate days, and to allow for occasional delays in telemetry. Three germinators each were also programmed to maintain constant temperature conditions of 10 and 25°C over the course of the experiment. The constant temperature treatments were implemented to track any changes in inherent germinability over the course of the experiment.

Germination vials were loaded into the environmental chambers on the day simulating 1 April, and every 10 d thereafter for a total of six simulated planting dates in each year. A set of germination vials were also loaded into the constant-temperature chambers on these dates. Germination vials were replicated three times within each chamber, and each temperature regime was replicated in three separate chambers. Each germination vial contained 30 seeds of a given species except for Sandberg bluegrass vials which contained 35 seeds. Germination vials were monitored every second day for 28 d and the seeds were counted and removed when they exhibited radicle extension of $\geqslant 2$ mm.

Treatment comparisons

Treatment means were analysed by analysis of variance for three performance indices: total percentage germination (G); days required to reach 50% germination for the laboratory data (D_{50}); and total percentage emergence for the field data (E). Days to 50% germination was based on the total number of seeds in the vial. Data were transformed to stabilize the variances using square root (D_{50}) and arcsine square root (G, E) transformations.

Cumulative germination models and historical simulation

A germination model was derived for primed and non-primed seeds of each species in each year from the variable-temperature laboratory-germination data (Arnold, 1959; Garcia-Huidobro *et al.*, 1982). Germination counts were pooled by species and priming treatment within each

chamber and the within-box totals considered replicate samples for model development and analysis. Cumulative germination was calculated for every species and priming treatment for every day of the germination test. Cumulative germination data were numerically transformed to a scale of 0 to 100% by dividing cumulative germination percentages by a scaling factor (Ellis *et al.*, 1986). The scaling factor was equal to the maximum-mean-germination percentage achieved in the optimal-temperature treatment for a given species. Application of the scaling factor adjusted the germination percentages for each species to a common scale with a maximum value of 100%.

For modelling purposes, the seed populations were considered to be composed of subpopulations based on relative germination rate (Garcia-Huidobro *et al.*, 1982; Benech Arnold *et al.*, 1990). Days required to achieve 5 to 95% germination were calculated for each species, year, planting date and priming treatment by interpolation from the cumulative-germination curves (Covell *et al.*, 1986). These percentile rankings were assumed to represent subpopulations that would germinate in the same relative order regardless of thermal environment (Garcia-Huidobro *et al.*, 1982). Inverse days required to achieve a given germination percentile was, therefore, considered to equal the per-day germination rate of the subpopulation represented by that percentile ranking.

Germination response data from the simulated field-temperature treatments were used to derive thermal-response rate equations for each species, year, priming treatment and subpopulation following the coefficient of variation (CV) procedure outlined by Arnold (1959). Thermal-time (θ) was defined as the number of degree-days above a base temperature (T_b) required for a given subpopulation to germinate. Per-day germination rate for a given subpopulation was related to θ and T_b with the following equation

$$R = (\bar{T} - T_b)\theta^{-1} \quad (1)$$

where R is germination rate (d^{-1}) and $\bar{T}$ is the mean temperature between time of sowing and germination. This equation was modified to give:

$$\theta = (\bar{T} - T_b)d \quad (2)$$

where d equals the number of days required for a given subpopulation to germinate.

Germination times for each subpopulation were determined for each thermal regime by interpolation from cumulative germination curves as previously described. Degree-day requirements for germination (θ) of a given subpopulation were iteratively calculated using a series of T_b estimates in 0·1°C increments between −10 and 10°C. The optimal value of T_b for a given subpopulation was estimated to be the temperature that resulted in the lowest CV for θ across all variable-temperature regimes (Arnold, 1959).

Equations (1) and (2) are only valid for temperatures greater than the estimated value of T_b. Time spent below T_b was not included in either the calculation of germination time or the estimation of $\bar{T}$.

Inclusion of planting dates 5 and 6 introduced high variability in T_b and θ estimates. This probably resulted from significant time spent in the supra-optimal temperature range for these species (Hardegree *et al.*, 1999). Optimized values of T_b and θ were recalculated using only planting dates 1–4 to characterize the sub-optimal temperature response.

Soil temperature data from the Orchard site were used in conjunction with thermal-model parameters to simulate late-winter/early-spring germination patterns for the period between 1993 and 1998. Field-temperatures measured at a depth of 1 cm in field-emergence plots in the sandy-loam site were used to simulate potential germination response of primed and non-primed seeds planted between 1 March and 15 May.

RESULTS

Average-daily temperature at 1 cm for the 6-year period remained below 2°C until the end of February, after which temperatures rose at a rate of approx. 0·18°Cd^{-1} for the next 3·5 months (Fig. 1). Laboratory germinators were programmed not to exceed the temperature range of 2 to 40°C. Field temperatures exceeded the low-temperature limit of the chambers (Fig. 2) for only a few days in 1993. Laboratory germinators were unable to match some high temperatures later in 1993 when the rate of temperature change in the field exceeded the rate at which the environmental chambers could heat during parts of the day. Field and laboratory temperature regimes were more accurate in 1994.

Total percentage germination in the laboratory did not vary significantly among simulated-site temperature regimes, so data were pooled across site treatments (Table 1). Priming had relatively little effect on total-laboratory germination across all treatments (Table 1,

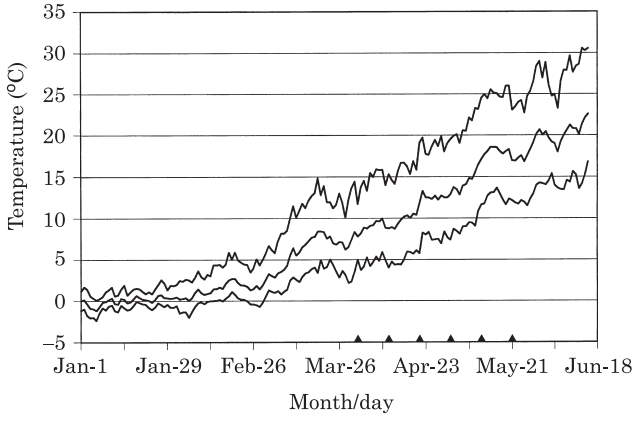

FIG. 1. Mean average, minimum and maximum temperatures measured at a depth of 1 cm in the sandy loam soil type at the Orchard Field Test site between 1993 and 1998. Arrows indicate planting dates for 1993–1994 field/laboratory study.

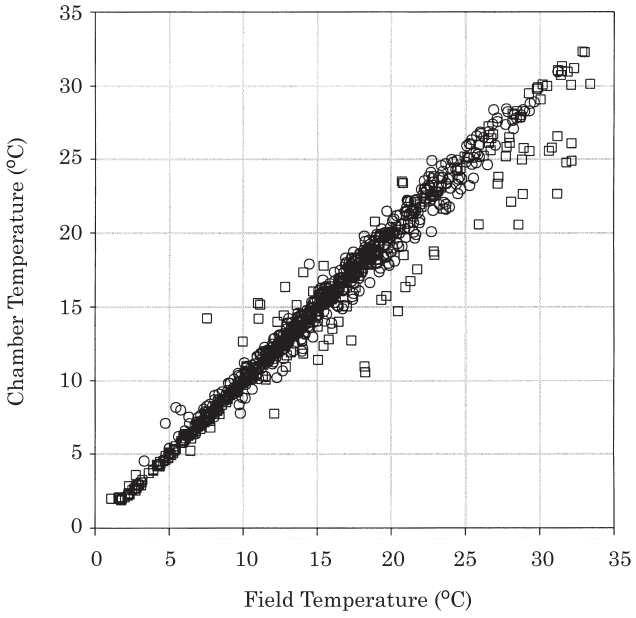

FIG. 2. Relative conformance between hourly field temperatures and temperatures measured inside laboratory germinators simulating 1 cm depth on the sandy loam soil type in 1993 (□) and 1994 (○). Only every fourth data point is shown to improve clarity.

Fig. 3). There was a slight tendency for total germination to decrease as the planting season progressed, but this was found to be significant in only a few cases. In the constant temperature treatments, planting date had a significant effect on total germination for some species but the magnitude of this effect was relatively small (Table 2). Priming had a relatively large negative effect on total germination for Sandberg bluegrass at 25°C in 1994.

Total percentage emergence was highly variable in the field (Table 3; Fig. 3). Total emergence was generally low or zero for the later planting dates in 1994 (Table 3, Fig. 3). Priming significantly increased total emergence for all species except Sandberg bluegrass in most years when evaluated across planting dates (Table 3). Site effects on emergence were relatively inconsistent, but on the coarse-textured site (loamy sand, site 2) emergence tended to be maximal on the first planting date, after which it dropped rapidly. Maximum emergence on the finer-textured site (silt loam, site 3) tended to be associated with relatively lower values of total emergence on the first planting date and higher values later in the season (Table 3). Field emergence was relatively lower for all seedlots and treatments in 1994.

Days required for 50% germination in the laboratory were significantly reduced (germination rate increased) by priming, and the effect was most notable in the earlier, cooler temperature treatments (Tables 4, 5, Fig. 3). Days to 50% emergence in the field was not very useful as a comparative rate index as the majority of field treatments did not result in 50% emergence. Emergence rates, however, were increased for earlier-germinating subpopulations, especially in the earlier-season planting treatments (Fig. 3).

Table 6 lists the optimized germination model parameters derived from the laboratory germination data. Germination data from planting dates 5 and 6 were not used in the CV analysis because temperatures routinely exceeded optimal temperature limits which were estimated to be in the 20–25°C range (Hardegree and Van Vactor,

TABLE 1. *Total germination percentage as a function of species, year, priming treatment and simulated planting date for the field-variable temperature treatments*

Species	Year	Priming treatment	Simulated planting date					
			1 Apr	11 Apr	21 Apr	1 May	11 May	21 May
Thickspike Wheatgrass	93†	Non-P	92 (3)	91 (3)	88 (3)	89 (3)	89 (4)	90 (3)
		Primed	91 (3)	89 (4)	88 (3)	89 (2)	89 (3)	90 (3)
	94‡	Non-P	69 (5)	66 (4)	69 (7)	67 (3)	64 (5)	63 (4)
		Primed	60 (6)	62 (5)	59 (5)	59 (8)	66 (5)	56 (6)
Bluebunch Wheatgrass	93†	Non-P	82 (3)	80 (3)	79 (4)	75 (5)	79 (5)	75 (7)
		Primed	86 (4)	*	80 (5)	78 (4)	73 (7)	69 (18)
	94‡	Non-P	83 (4)	82 (7)	88 (4)	81 (4)	84 (4)	83 (4)
		Primed	80 (4)	81 (4)	77 (6)	84 (3)	77 (9)	76 (6)
Sandberg Bluegrass	93†	Non-P	74 (5)	76 (6)	72 (7)	70 (3)	72 (6)	68 (8)
		Primed	67 (8)	76 (7)	77 (8)	69 (8)	72 (5)	75 (8)
	94	Non-P	69 (8)	71 (8)	67 (7)	71 (5)	74 (6)	78 (6)
		Primed	67 (7)	67 (6)	54 (12)	70 (4)	69 (4)	71 (5)
Bottlebrush Squirreltail	93†‡	Non-P	78 (5)	82 (2)	77 (4)	77 (4)	77 (5)	80 (7)
		Primed	79 (2)	78 (6)	84 (4)	77 (5)	76 (3)	79 (7)
	94†	Non-P	71 (7)	77 (6)	72 (5)	71 (7)	72 (7)	74 (5)
		Primed	77 (6)	76 (6)	71 (5)	69 (3)	73 (5)	69 (11)

Site diferences were not significant,therefore, data were pooled. Numbers in parentheses represent s.e.m.
* Missing data.
† Priming treatment did not have a significant effect on total germination percentage in this year.
‡ Planting date did not have a significant effect on total germination percentage in this year.

TABLE 2. *Total germination percentage as a function of species, year, priming treatment and simulated planting date for the constant 10 and 25°C treatments*

Species	Year	Temperature	Planting date	Priming treatment	
				Non-primed	Primed
Thickspike Wheatgrass	93†‡	10	1–6	90 (5)	90 (3)
		25	1–6	90 (4)	88 (4)
	94	10	1–6	64 (7)	59 (6)
		25	1–6	57 (6)	50 (5)
Bluebunch Wheatgrass	93‡	10	1–6	82 (5)	81 (5)
		25	1–6	75 (10)	73 (9)
	94	10	1–6	83 (5)	78 (5)
		25	1–6	81 (5)	70 (7)
Sandberg Bluegrass	93†‡	10	1–6	70 (7)	69 (5)
		25	1–6	69 (8)	69 (9)
	94	10	1–6	69 (6)	69 (7)
		25	1–6	66 (8)	50 (8)
Bottlebrush Squirreltail	93†	10	1	75 (2)	82 (1)
			2	77 (5)	82 (4)
			3	72 (6)	78 (4)
			4	76 (8)	75 (6)
			5	68 (4)	81 (1)
			6	74 (5)	79 (4)
			1–6	74 (5)	79 (4)
		25	1	84 (2)	84 (2)
			2	77 (4)	82 (2)
			3	78 (3)	87 (5)
			4	65 (5)	79 (5)
			5	77 (1)	77 (3)
			6	81 (3)	73 (3)
			1–6	77 (7)	80 (6)
	94‡	10	1–6	74 (3)	73 (5)
		25	1–6	66 (5)	62 (6)

Planting date effects were not significantly different except for bottlebrush squirreltail in 1993. Data for other species and years were, therefore, pooled across simulated planting dates. Numbers in parentheses represent s.e.m.

† Temperature treatment did not have a significant effect on total germination percentage in this year.

‡ Priming treatment did not have a significant effect on total germination percentage in this year.

1999; Hardegree *et al.*, 1999). Priming significantly decreased θ for almost all species, seedlots and subpopulations. Optimized values of T_b were generally lower for primed seeds. T_b also tended to decrease as subpopulation percentage increased. Bottlebrush squirreltail exhibited a somewhat anomalous priming effect in 1994 with a relatively small reduction in θ and large reduction in T_b (Table 6).

The field-temperature data for the period 1993–1998 were used to derive model estimates of days to 50% germination for simulated planting dates between 1 March and 15 May. The difference between simulated values for primed and non-primed seeds is shown in Fig. 4. Figure 4 also shows measured values of germination time used to derive model parameters for this subpopulation. This figure illustrates the magnitude of the potential priming effect under a wider range of temperature conditions than were measured in this experiment.

DISCUSSION

Seed priming has been shown to advance germination and emergence rate for many agricultural plant species (e.g. Brocklehurst *et al.*, 1984; Helsel *et al.*, 1986; Alvarado *et al.*, 1987; Evans and Pill, 1989; Bradford *et al.*, 1990; Khan *et al.*, 1992; Suzuki and Obayashi, 1994; Yamamoto *et al.*, 1997). Significant germination enhancement at low temperature has been measured for primed seeds of several range grass species, but previous studies have not evaluated germination and emergence under field conditions (Hardegree and Emmerich, 1992; Hardegree, 1994*a*,*b*, 1996; Mueller, 1996). This study showed that seed priming enhanced total emergence of four bunchgrass species in the field, but that the priming effect was highly dependent upon seedlot, planting date and soil type (Table 3, Fig. 3). Priming also enhanced germination and emergence rates, but significant advancement was mostly limited to the earlier, cooler, planting dates (Table 4, Fig. 3).

The most likely cause of the discrepancy between germination and emergence data is water-stress and soil physical constraints. These effects are exacerbated as temperatures warm and the soil becomes subject to greater evaporative stress later in the season (Hegarty, 1973; Brar *et al.*, 1992; Finch-Savage and Phelps, 1993; Egli and TeKrony, 1996; Helms *et al.*, 1996; Weaich *et al.*, 1996). Hand watering every other day was not sufficient to keep

TABLE 3. *Total percentage emergence as a function of species, year, priming treatment, site and simulated planting date*

Species	Year	Priming treatment	Site	Simulated planting date					
				1 Apr	11 Apr	21 Apr	1 May	11 May	21 May
Thickspike Wheatgrass	93	Non-P	1	91 (14)	75 (16)	67 (19)	83 (24)	35 (26)	64 (19)
			2	88 (4)	68 (26)	47 (7)	50 (10)	10 (16)	12 (9)
			3	38 (18)	55 (9)	45 (11)	28 (15)	31 (17)	66 (14)
		Primed	1	88 (12)	74 (19)	96 (7)	74 (9)	47 (8)	77 (11)
			2	80 (13)	62 (5)	66 (4)	62 (16)	10 (8)	20 (7)
			3	55 (11)	70 (11)	68 (8)	58 (11)	49 (18)	87 (11)
	94†	Non-P	1	43 (2)	4 (8)	36 (9)	2 (3)	0 (0)	0 (0)
			2	12 (11)	1 (1)	6 (3)	5 (8)	0 (0)	0 (0)
			3	22 (3)	29 (16)	20 (9)	2 (1)	5 (5)	0 (0)
		Primed	1	26 (8)	12 (10)	55 (7)	2 (2)	3 (4)	1 (2)
			2	23 (2)	6 (6)	8 (3)	1 (1)	1 (1)	0 (0)
			3	19 (8)	34 (1)	27 (9)	10 (12)	9 (12)	5 (8)
Bluebunch Wheatgrass	93	Non-P	1	49 (11)	61 (5)	64 (9)	57 (11)	35 (9)	58 (11)
			2	62 (11)	67 (1)	36 (7)	33 (8)	3 (1)	22 (13)
			3	27 (9)	48 (13)	49 (14)	30 (22)	40 (12)	40 (11)
		Primed	1	91 (9)	70 (7)	71 (11)	74 (8)	42 (15)	60 (6)
			2	77 (6)	74 (*)	54 (1)	51 (11)	8 (2)	24 (15)
			3	22 (7)	55 (6)	79 (14)	29 (10)	48 (11)	70 (24)
	94	Non-P	1	50 (11)	5 (3)	41 (15)	4 (7)	9 (14)	0 (1)
			2	33 (31)	12 (8)	15 (11)	1 (1)	0 (1)	0 (0)
			3	40 (4)	31 (4)	59 (8)	7 (5)	36 (6)	1 (2)
		Primed	1	41 (12)	13 (14)	55 (22)	1 (1)	3 (2)	1 (1)
			2	35 (19)	10 (6)	24 (15)	0 (0)	2 (3)	0 (0)
			3	46 (5)	44 (6)	56 (5)	10 (18)	19 (27)	2 (2)
Sandberg Bluegrass	93†	Non-P	1	41 (19)	54 (10)	17 (5)	20 (9)	13 (11)	40 (5)
			2	48 (10)	34 (3)	30 (13)	15 (13)	12 (15)	25 (10)
			3	20 (14)	36 (12)	26 (9)	4 (8)	23 (4)	39 (19)
		Primed	1	43 (22)	39 (2)	55 (1)	30 (7)	14 (18)	50 (14)
			2	66 (18)	40 (13)	28 (19)	15 (14)	2 (3)	26 (5)
			3	18 (10)	32 (5)	27 (15)	5 (3)	31 (3)	47 (12)
	94†	Non-P	1	21 (8)	18 (17)	14 (13)	2 (3)	0 (0)	0 (0)
			2	24 (2)	19 (7)	12 (11)	4 (8)	0 (0)	0 (0)
			3	15 (3)	15 (13)	5 (5)	2 (1)	0 (1)	0 (0)
		Primed	1	18 (3)	11 (9)	17 (15)	2 (2)	1 (2)	0 (0)
			2	41 (9)	18 (8)	8 (6)	6 (11)	1 (1)	0 (0)
			3	20 (13)	4 (1)	1 (1)	0 (0)	0 (0)	0 (0)
Bottlebrush Squirreltail	93	Non-P	1	60 (14)	60 (13)	55 (13)	45 (5)	26 (12)	58 (6)
			2	74 (6)	60 (12)	53 (9)	71 (13)	12 (13)	29 (27)
			3	12 (3)	47 (7)	30 (10)	19 (9)	37 (14)	59 (5)
		Primed	1	68 (7)	67 (*)	80 (14)	52 (9)	42 (1)	66 (13)
			2	75 (1)	75 (7)	53 (21)	40 (9)	9 (11)	24 (9)
			3	21 (0)	54 (15)	27 (7)	20 (5)	55 (27)	67 (12)
	94‡	Non-P	1	31 (13)	28 (19)	55 (12)	7 (9)	12 (10)	1 (2)
			2	35 (13)	9 (12)	18 (21)	2 (1)	0 (1)	0 (0)
			3	35 (9)	36 (4)	30 (13)	19 (21)	10 (3)	1 (1)
		Primed	1	40 (11)	15 (14)	59 (10)	0 (0)	9 (9)	6 (4)
			2	60 (16)	42 (26)	32 (25)	2 (2)	2 (3)	0 (1)
			3	29 (10)	36 (11)	39 (7)	25 (21)	22 (21)	2 (4)

Soil types for sites 1–3 were sandy loam, loamy sand and silt loam, respectively. Numbers in parentheses represent s.e.m.
* Standard error of the mean could not be calculated because only one replicated field plot was planted.
† Priming treatment differences not significant in this year.
‡ Site differences not significant in this year.

the soil wet at the planting depth as the season progressed, particularly in 1994. Mean temperature (at a depth of 1 cm) among the three soils did not differ by more than a few degrees, but priming effects on emergence were significantly affected by differences in soil type (Table 3). Soil textural effects were probably manifest through their influence on near-surface soil-hydraulic properties. The loamy sand (site 2) would lose moisture most rapidly to drainage and has a much lower water holding capacity than either the sandy loam or silt loam. Seeds that germinate quickly are more likely to emerge before water became limiting. Priming effects on total percentage germination were not apparent in the laboratory where water was not limiting (Table 1). Year effects may have contributed to the lower

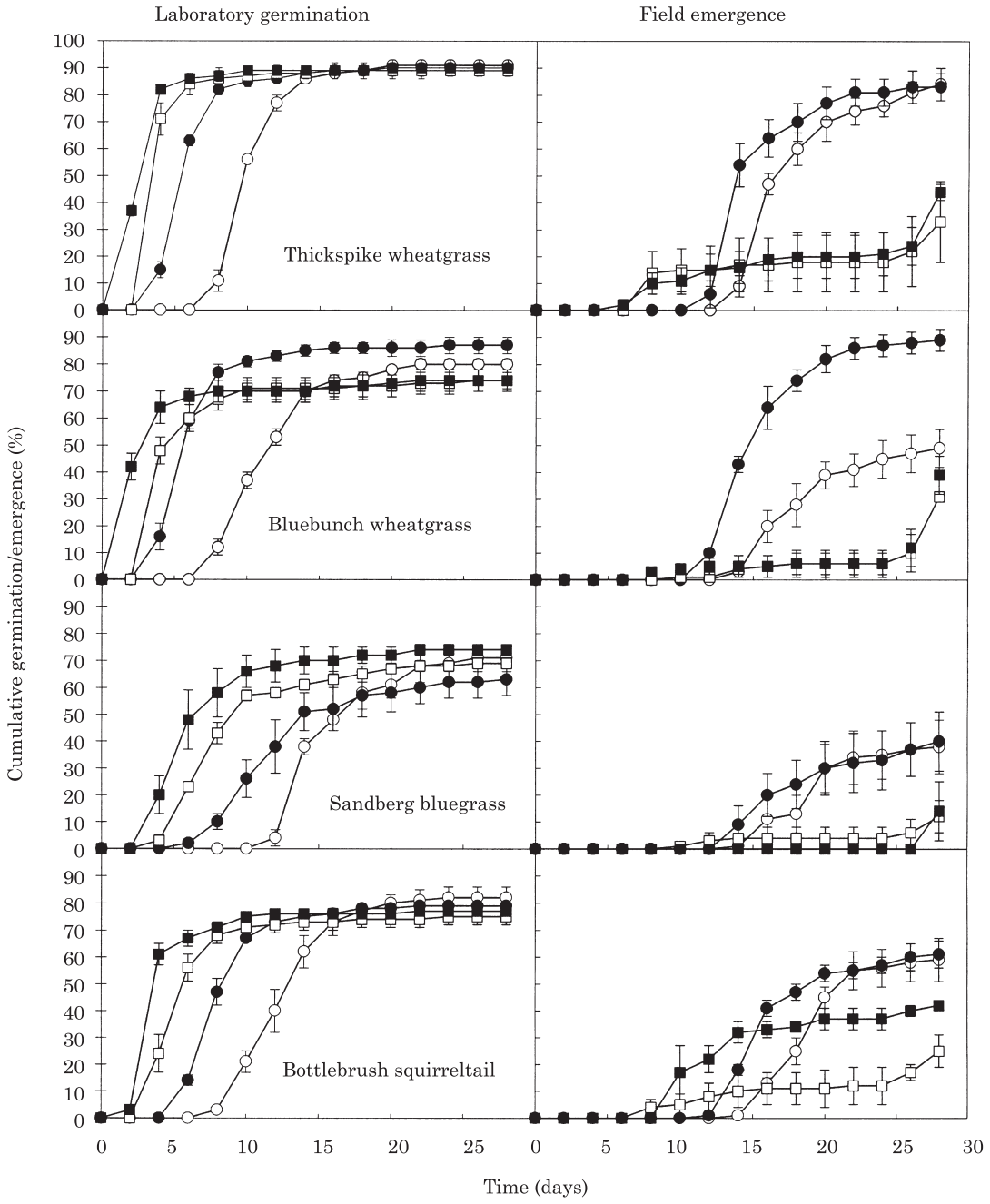

FIG. 3. Cumulative laboratory germination and field emergence of primed (■, ●) and non-primed (□, ○) seeds for planting dates 1 April (○, ●) and 11 May (□, ■) for the sandy loam temperature regime and field site. Bars represent ±s.e.

overall emergence in 1994, but this appears to be a factor only for Thickspike wheatgrass which showed lower total germination percentage in the laboratory during the second year (Table 1).

Laboratory simulation of the field-thermal environment allowed us to separate temperature effects from other environmental factors that influence germination and emergence. The data from this experiment show a consistent pattern of priming effects on thermal response across simulated plant dates and across seed subpopulations. Primed seeds germinated more rapidly and the magnitude of this effect was larger under low-temperature conditions (Table 3, Fig. 3). We quantified the priming effect by calculating thermal-response parameters from the sub-optimal temperature data (Table 6). Priming significantly lowered thermal time requirements for germination and resulted in lower base temperatures for germination across most subpopulations (Table 6). Germination model parameters from the laboratory simulation also allowed us to extrapolate to other thermal conditions such as those

TABLE 4. *Days to 50% germination as a function of species, year, priming treatment, site-temperature regime and simulated planting date*

Species	Year	Priming treatment	Site	Simulated planting date					
				1 Apr	11 Apr	21 Apr	1 May	11 May	21 May
Thickspike Wheatgrass	93	Non-P	1	9·7 (0·1)	9·2 (0·2)	6·8 (0·2)	6·9 (0·0)	3·4 (0·2)	3·6 (0·2)
			2	8·5 (0·4)	7·9 (0·3)	5·6 (0·2)	5·5 (0·4)	3·4 (0·1)	3·2 (0·1)
			3	10·2 (0·5)	9·2 (0·3)	6·8 (0·4)	6·5 (0·6)	3·3 (0·1)	3·7 (0·1)
		Primed	1	5·4 (0·1)	5·4 (0·4)	4·3 (0·5)	3·8 (0·3)	2·5 (0·1)	2·7 (0·6)
			2	5·0 (0·2)	5·0 (0·1)	3·6 (0·1)	3·1 (0·1)	2·0 (0·5)	2·3 (0·2)
			3	5·5 (0·3)	5·7 (0·3)	4·5 (0·3)	3·8 (0·3)	2·4 (0·4)	2·8 (0·3)
	94†	Non-P	1	11·0 (0·7)	7·8 (0·2)	7·2 (0·3)	6·1 (0·4)	6·1 (1·2)	6·0 (0·7)
			2	9·2 (0·9)	8·3 (0·5)	6·6 (1·1)	6·3 (1·1)	6·3 (2·1)	5·9 (1·4)
			3	11·1 (0·9)	8·4 (0·2)	7·1 (1·4)	6·5 (1·1)	5·7 (1·1)	6·0 (1·4)
		Primed	1	6·7 (1·8)	6·2 (1·2)	4·7 (1·2)	4·9 (0·9)	3·3 (0·4)	4·0 (0·3)
			2	6·2 (0·6)	6·0 (0·3)	4·8 (1·5)	5·4 (1·4)	3·7 (0·6)	5·2 (1·2)
			3	6·6 (1·4)	6·4 (0·2)	4·1 (0·2)	4·8 (1·4)	3·5 (0·3)	4·5 (1·5)
Bluebunch Wheatgrass	93	Non-P	1	11·2 (0·5)	10·4 (0·6)	7·4 (0·1)	8·5 (0·7)	4·3 (0·6)	3·8 (0·1)
			2	10·2 (0·7)	8·8 (0·4)	6·3 (0·5)	6·3 (0·7)	3·6 (0·1)	3·8 (0·1)
			3	11·9 (0·5)	10·1 (0·5)	7·5 (0·4)	7·7 (0·8)	4·1 (0·8)	4·6 (1·0)
		Primed	1	5·4 (0·2)	*	4·6 (0·5)	3·8 (0·3)	2·5 (0·8)	3·3 (0·8)
			2	5·0 (0·1)	*	3·8 (0·5)	3·3 (0·5)	2·7 (0·8)	‡
			3	5·5 (0·2)	*	4·3 (0·7)	4·2 (0·8)	2·7 (0·5)	2·9 (0·8)
	94	Non-P	1	6·3 (0·5)	5·7 (0·1)	4·7 (1·0)	4·4 (0·3)	3·7 (0·6)	3·4 (0·2)
			2	5·8 (0·3)	5·7 (0·4)	3·6 (0·4)	4·1 (0·4)	3·5 (0·4)	3·5 (0·1)
			3	6·6 (0·8)	6·3 (0·4)	3·7 (0·2)	4·4 (0·5)	3·5 (0·3)	3·6 (0·1)
		Primed	1	2·6 (0·3)	3·5 (0·3)	2·4 (0·7)	2·4 (0·3)	3·2 (1·0)	3·0 (0·5)
			2	2·4 (0·6)	3·5 (0·1)	2·2 (0·5)	2·2 (0·6)	2·2 (0·6)	2·4 (0·8)
			3	3·0 (0·3)	3·7 (0·3)	1·9 (0·3)	2·3 (0·4)	2·7 (0·7)	2·4 (0·7)
Sandberg Bluegrass	93	Non-P	1	15·3 (1·5)	13·2 (1·0)	10·5 (1·3)	10·4 (0·4)	8·0 (0·5)	7·9 (0·2)
			2	13·4 (0·1)	11·9 (0·9)	9·5 (1·7)	9·4 (0·3)	7·3 (1·6)	8·2 (1·9)
			3	15·0 (1·0)	13·1 (0·8)	10·9 (0·8)	10·3 (0·4)	7·1 (0·7)	7·3 (0·3)
		Primed	1	12·7 (2·0)	11·4 (1·1)	8·0 (0·4)	9·3 (1·4)	6·1 (1·9)	5·8 (1·2)
			2	10·5 (0·3)	9·9 (0·7)	7·3 (0·1)	7·5 (1·0)	7·1 (1·8)	7·3 (3·0)
			3	12·5 (1·8)	11·0 (0·1)	9·2 (2·6)	9·3 (0·8)	5·9 (0·5)	6·0 (0·9)
	94†	Non-P	1	12·9 (1·7)	9·1 (0·3)	9·8 (1·7)	8·2 (0·5)	7·5 (0·3)	6·8 (0·4)
			2	12·2 (0·8)	9·8 (0·4)	9·2 (0·5)	8·0 (0·5)	7·2 (0·7)	7·0 (0·2)
			3	13·2 (0·3)	9·7 (0·2)	9·9 (0·8)	8·0 (0·8)	7·9 (0·7)	7·4 (0·2)
		Primed	1	10·4 (1·8)	8·5 (1·2)	‡	5·6 (0·2)	8·0 (1·8)	6·2 (0·7)
			2	9·5 (2·3)	7·4 (0·5)	8·6 (2·2)	6·3 (0·9)	7·7 (0·4)	5·3 (0·6)
			3	9·8 (2·4)	7·8 (0·8)	9·9 (3·5)	5·5 (0·5)	8·0 (1·8)	5·6 (0·5)
Bottlebrush Squirreltail	93	Non-P	1	12·5 (1·1)	11·6 (0·3)	9·4 (1·1)	9·4 (0·4)	5·3 (0·6)	5·3 (0·2)
			2	11·6 (0·3)	10·2 (0·4)	7·7 (0·1)	8·0 (0·6)	4·8 (0·9)	5·0 (0·4)
			3	13·2 (0·7)	11·6 (0·3)	9·0 (0·2)	9·2 (0·3)	5·0 (0·1)	5·3 (0·4)
		Primed	1	8·0 (0·5)	8·5 (0·3)	5·6 (0·3)	5·4 (0·1)	3·5 (0·2)	3·4 (0·1)
			2	6·9 (0·4)	7·0 (0·6)	4·9 (0·5)	5·1 (0·3)	3·5 (0·3)	4·0 (1·1)
			3	7·9 (0·6)	8·2 (1·1)	5·7 (0·4)	6·0 (0·6)	4·0 (0·6)	3·6 (0·5)
	94†	Non-P	1	10·7 (2·4)	7·8 (0·8)	7·3 (1·5)	5·6 (0·3)	4·1 (0·6)	4·3 (0·4)
			2	9·7 (3·1)	7·7 (0·4)	7·3 (0·9)	6·7 (2·0)	5·5 (0·5)	4·6 (0·3)
			3	9·7 (0·5)	7·4 (0·3)	6·1 (0·2)	6·3 (0·8)	4·5 (1·1)	4·5 (0·3)
		Primed	1	4·3 (0·7)	5·1 (0·6)	3·7 (0·1)	4·0 (0·2)	3·0 (0·8)	6·8 (1·4)
			2	5·1 (0·3)	5·3 (0·3)	3·8 (0·1)	4·2 (0·3)	3·2 (0·6)	3·9 (1·4)
			3	5·0 (0·7)	5·2 (0·3)	4·5 (1·6)	4·3 (0·2)	2·7 (0·3)	3·7 (0·5)

Numbers in parentheses represent s.e.m.
* Missing data.
† Site differences not significant in this year.
‡ Treatment did not reach 50% germination.

measured at the Orchard site earlier in the season and in other years (Fig. 4). Under conditions where water was available, greater germination advancement would be expected for primed seeds that had been planted earlier than 1 April during the 2 years of our field experiment (Fig. 4).

Later germinating subpopulations exhibited relatively higher variability in germination and emergence response (Table 6). This increased variability was exhibited most strongly at supraoptimal temperatures as has been shown previously for non-primed seeds of these species and seedlots (Hardegree *et al.*, 1999). This effect was most

TABLE 5. *Days to 50% germination as a function of species, year, priming treatment and simulated planting date for the constant 10 and 25°C treatments*

Species	Year	Temperature	Planting date	Priming treatment	
				Non-primed	Primed
Thickspike Wheatgrass	93	10	1–6	7·7 (0·5)	4·2 (0·4)
		25	1–6	3·1 (0·2)	1·9 (0·4)
	94	10	1–6	10·9 (1·9)	7·5 (2·5)
		25	1–6	6·0 (2·1)	†
Bluebunch Wheatgrass	93	10	1	9·0 (1·1)	4·4 (0·3)
			2	9·2 (1·2)	*
			3	7·9 (0·5)	4·5 (0·3)
			4	9·2 (1·5)	4·7 (0·7)
			5	8·5 (0·3)	4·8 (0·6)
			6	7·7 (0·4)	5·3 (0·2)
			1–6	8·6 (1·0)	4·7 (0·5)
		25	1	3·6 (0·2)	2·0 (0·6)
			2	3·8 (0·4)	*
			3	3·2 (0·2)	1·6 (0·3)
			4	3·7 (0·6)	2·6 (1·2)
			5	3·5 (0·2)	1·8 (0·5)
			6	4·0 (1·1)	4·9 (3·0)
			1–6	3·6 (0·6)	2·6 (1·7)
	94	10	1–6	6·5 (0·6)	3·5 (0·6)
		25	1–6	2·9 (0·3)	1·9 (0·7)
Sandberg Bluegrass	93	10	1–6	13·0 (1·5)	10·5 (1·3)
		25	1–6	7·2 (1·2)	6·7 (1·5)
	94	10	1–6	12·2 (1·3)	8·3 (1·2)
		25	1–6	7·2 (1·1)	†
Bottlebrush Squirreltail	93	10	1–6	10·3 (0·7)	6·1 (0·5)
		25	1–6	4·3 (0·7)	3·1 (0·6)
	94	10	1–6	8·7 (1·1)	5·4 (0·6)
		25	1–6	4·2 (0·8)	3·7 (1·7)

Planting date effects were not significantly different except for bluebunch wheatgrass in 1993. Data for other species and years were, therefore, pooled across simulated planting dates. Numbers in parentheses represent s.e.m.

* Missing data.

† Some treatment replicates did not reach 50% germination.

apparent in the small-seeded Sandberg bluegrass which is generally slower to germinate and perhaps more susceptible to respiratory losses during priming and at supraoptimal temperatures. Sandberg bluegrass showed significant reduction in total percentage germination at a constant 25°C (Table 2). Hardegree *et al.* (1999) showed that the optimal temperature for 50% germination of non-primed Sandberg bluegrass seeds was about 20°C, 5°C lower than that for the other species examined. Decreased germination at supraoptimal temperatures is generally attributed to membrane degradation, denaturation of enzymes and other degenerative processes (Bewley and Black, 1994).

Ellis and Butcher (1988) and Dahal *et al.* (1990) also investigated priming effects on thermal germination response. They too found that priming decreased thermal-time requirements but results differed in whether priming reduced base temperature thresholds for germination. Both previous studies calculated thermal model parameters by regression from constant-temperature germination data but did not test their models under variable temperature conditions.

Mueller (1996) noted that seedling root growth was diminished for primed seeds of four other cool-season grass species. Mueller (1996), however, conducted both his priming and germination experiments under conditions that reached 30°C during the day. This temperature was found to be supraoptimal for non-primed seeds of the same species used in the current experiment (Hardegree *et al.*, 1999). Supraoptimal temperatures can be expected to accelerate degradative metabolic processes that affect subsequent growth (Bewley and Black, 1994). Priming effects on germination rate are also known to be reduced at higher temperatures (Taylor *et al.*, 1998), therefore, the relative benefit of priming was also minimized in Mueller's (1996) experiment.

The major thrust of many previous germination-response studies has been to use thermal-model parameters as indices for comparison of seedlots (Covell *et al.*, 1986; Ellis *et al.*, 1986; Benech Arnold *et al.*, 1990; Fidanza *et al.*, 1996; Holshouser *et al.*, 1996). We also developed thermal-model parameters (Table 6) but our objective was to compare actual and predicted responses under alternative field-temperature scenarios. Arnold (1959) argued that it was desirable to minimize variability in model coefficients but that the ultimate modelling objective was to minimize the residual predictive error in germination time (measured in

TABLE 6. *Thermal model parameters calculated from field-variable temperature data from the first four planting dates in 1993 and 1994*

		1993				1994			
		Non-Primed		Primed		Non-primed		Primed	
Species	Subpopulation	T_b	θ	T_b	θ	T_b	θ	T_b	θ
Thickspike Wheatgrass	10	2·2	43·6 (0·5)	−1·7	29·6 (1·6)	3·2	45·8 (1·0)	0·0	25·9 (0·8)
	20	1·8	50·2 (0·5)	−0·5	33·6 (0·7)	2·4	57·4 (0·9)	−4·5	48·3 (0·6)
	30	1·7	54·6 (0·2)	−0·8	39·3 (0·3)	2·3	63·4 (0·9)	−3·3	55·0 (0·5)
	40	1·0	62·9 (0·5)	−1·8	47·7 (0·5)	1·7	75·5 (1·3)	−1·3	59·0 (0·7)
	50	0·6	69·8 (0·5)	−2·0	53·9 (0·9)	1·3	87·7 (1·6)	−2·8	80·9 (1·9)
	60	0·8	71·8 (0·6)	−3·2	65·9 (1·3)	−2·5	142·7 (3·7)	−4·2	126·8 (4·5)
	70	0·3	81·2 (0·8)	−3·2	75·4 (1·7)	−9·9	269·1 (9·8)	−3·6	203·6 (9·0)
	80	−0·7	100·9 (1·4)	−3·2	90·9 (2·6)				
Bluebunch Wheatgrass	10	2·0	46·2 (0·4)	1·1	22·6 (1·4)	3·8	27·6 (0·7)	6·5	4·6 (0·6)
	20	1·7	54·5 (0·3)	0·0	32·0 (0·6)	3·7	31·9 (0·4)	5·2	9·1 (0·9)
	30	0·9	64·5 (0·7)	−0·7	39·1 (0·4)	2·9	38·4 (0·5)	3·7	14·9 (0·9)
	40	0·8	70·5 (0·9)	−2·4	49·9 (0·4)	2·1	46·6 (0·6)	1·7	23·3 (0·9)
	50	0·4	80·2 (1·1)	−3·2	59·9 (1·0)	0·8	58·0 (1·1)	0·3	32·1 (0·9)
	60	−0·2	96·4 (1·8)	−8·9	97·9 (2·1)	−0·4	72·1 (1·8)	−6·2	59·6 (1·0)
	70	−5·2	169·1 (4·7)			−1·9	94·6 (2·3)	−2·7	61·4 (2·0)
	80					−6·5	158·4 (5·9)		
Sandberg Bluegrass	10	1·0	78·2 (0·9)	−2·4	76·8 (1·0)	1·1	78·6 (1·2)	2·2	38·6 (0·8)
	20	0·4	91·1 (0·9)	−2·0	85·2 (0·9)	−0·2	99·6 (1·4)	−0·2	60·9 (1·3)
	30	0·2	100·1 (0·9)	−1·4	89·0 (1·1)	−0·7	112·7 (1·4)	−1·4	78·8 (1·6)
	40	−0·6	114·1 (0·8)	−0·6	91·3 (1·0)	−1·1	126·0 (1·3)	−2·0	95·7 (2·5)
	50	−1·2	131·3 (0·7)	−0·9	103·7 (1·7)	−1·2	138·0 (1·4)	−2·1	115·3 (5·6)
	60	−1·7	149·9 (1·7)	−1·8	129·7 (3·8)	−2·3	166·9 (2·7)	−1·7	139·6 (9·0)
	70	−2·5	189·0 (3·6)			−1·7	190·7 (5·8)	1·8	139·6 (13·8)
Bottlebrush Squirreltail	10	1·1	62·3 (0·7)	−0·5	41·5 (0·9)	2·5	42·0 (1·4)	−5·5	40·7 (0·6)
	20	0·7	72·2 (0·7)	0·3	45·5 (1·0)	1·5	56·0 (1·0)	−5·7	52·1 (0·7)
	30	0·1	84·3 (0·7)	0·7	49·1 (0·7)	0·4	69·7 (0·8)	−4·8	58·1 (0·8)
	40	−0·3	94·5 (0·7)	0·3	56·9 (0·8)	−0·1	81·2 (1·0)	−5·6	71·1 (1·1)
	50	−0·5	104·2 (0·9)	0·3	62·1 (0·8)	0·6	88·0 (1·8)	−7·4	88·5 (1·5)
	60	−1·5	125·3 (0·8)	0·3	67·9 (1·1)	−0·5	116·8 (3·9)		
	70	−4·9	186·3 (2·6)	−0·3	81·5 (1·6)	−2·1	165·4 (6·7)		
	80			−4·0	150·4 (8·3)				

Base temperatures (T_b) for each subpopulation were determined to be optimal for minimizing variability in thermal time (θ) estimates as measured by the CV method (Arnold, 1959). Numbers in parentheses present s.e.m. for optimized values of θ.

days). We believe that this also applies to the analysis of comparative thermal response among species, seedlots and seed treatments. In this study, priming effects on germination model coefficients were determined to be statistically significant; however, priming effects on germination time were larger than a few days only for the cooler, earlier season planting dates (Table 4, Fig. 4). Modelling expanded the predictive range for potential priming response over the simulated test period (Fig. 4) and indicated that a larger effect would have manifest itself at earlier planting dates than measured in this experiment. We conclude that seed priming of these species is inappropriate unless planting can occur early enough in the spring to take advantage of a significant priming effect. In the Intermountain region of the western United States, these periods of cooler temperatures also coincide with the most likely period of water availability.

A major limitation to our analysis is that we did not evaluate response to water stress and the physical constraints of seedling emergence from soil. Although we added supplemental water to our field plots, emergence was severely restricted, regardless of priming treatment, later in the season. Further analysis of hydrothermal response, as has been carried out for some agricultural species (Ellis and Butcher, 1988; Dahal and Bradford, 1990; Dahal *et al.*, 1990) and additional field studies are needed before we will be able to predict annual variability in emergence under natural seedbed conditions. These studies should also include consideration of soil structural effects on seedling emergence (Weaich *et al.*, 1996).

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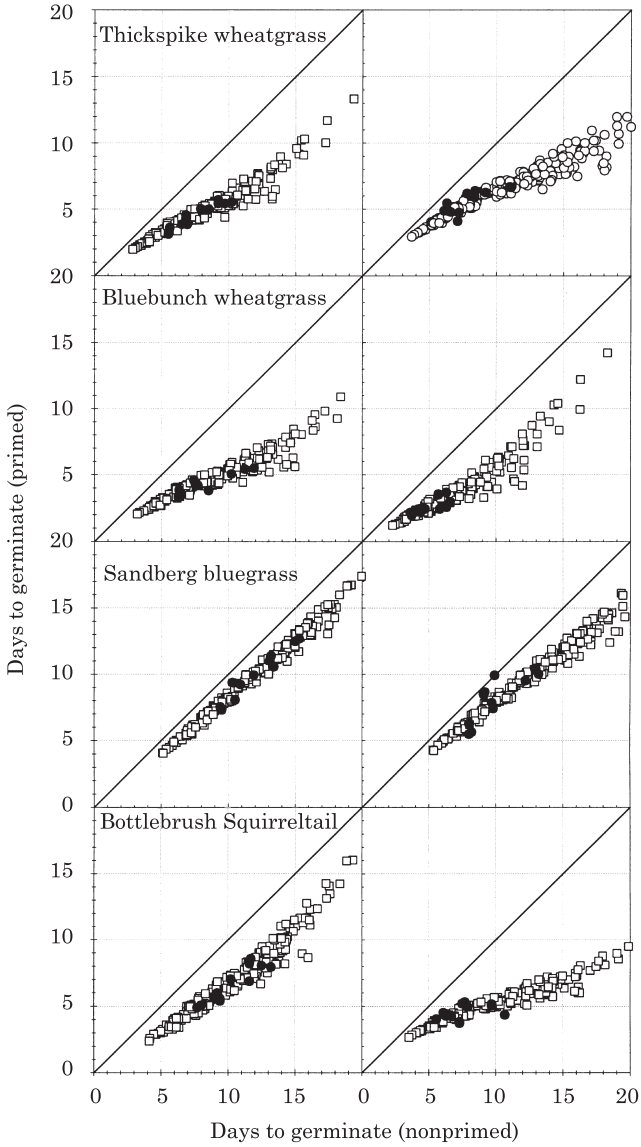

FIG. 4. Relationship between simulated days to 50% germination of primed and non-primed seeds for planting dates between 1 March and 15 May, 1993 to 1998 (□). Measured data points from the 1993/94 laboratory experiment used in construction of the predictive model (●).

product does not constitute endorsement by the USDA and does not imply its approval to the exclusion of other products that may also be suitable.

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